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## New Tertiary Teleosts from Argentina

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Our knowledge of the Tertiary fresh-water fishes of South America has been confined largely to the few forms described from several lacustrine deposits in Brazil. This assemblage of probably late Tertiary age is composed of a clupeid (*Knightia*), at least three characins (*Procharax*, *Lignobrycon*, and *Eobrycon*), an ariid (*Arius*), a serranid (*Percichthys*), and three cichlids (*Acara*, *Aequidens*, and *Macracara*). The clupeid, the ariid, and the serranid probably represent separate invasions by marine ancestors, of which only the ariid occurs in this region at the present time. The primary-division characins and the secondary-division cichlids are typical representatives of the modern neotropical fish fauna. In addition, (1) a *Percichthys* has been described from an Eocene deposit in Patagonia (Schaeffer, 1947b); (2) DeSaez (1941) has described several siluroids from the territory of Chubut, Argentina; and (3) Savage (1951) has reported lepidosirenid and siluroid fragments from Colombia.

Several years ago a series of Tertiary fishes from Salta Province in northern Argentina was sent to the American Museum of Natural History for identification and study. These specimens were obtained by Juan J. Zunino of the Yacimientos Petroliferos Fiscales and Enrique T. Mauri. They were forwarded to the Museum through the kindness of Dr. Pedro Stipanovic. The collection also includes some Cretaceous fishes which have not yet been studied, and the remains of a mammal and some chelonians which are unfortunately too fragmentary for positive identification.

The author is grateful to Dr. Bobb Schaeffer of the American Museum

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of Natural History for the opportunity to describe the Tertiary fishes. Although they offer no new evidence on the origin and dispersal of the existing South American fish fauna, these new discoveries help to round out our meager picture of the Tertiary fresh-water fishes in that continent. For their constructive criticisms of the manuscript, I am indebted to Dr. Bobb Schaeffer and Dr. Theodore Eaton of the University of Kansas. Dr. Errol I. White of the British Museum (Natural History) kindly supplied a photograph of the type of *Corydoras revelatus*. The photographs of the described specimens were taken by Mr. Elwood Logan.

### GEOLOGY AND PALEOECOLOGY

The sedimentary sequence in Salta Province is characterized by a series of subparallel, anticlinal ranges formed of lower and middle Paleozoic rocks covered, according to Harrington (1956), by continental Permian, marine, and continental Mesozoic, and more than 7000 meters of continental upper Miocene and Pliocene, sediments.

The fishes described in the present paper were found in two different stratigraphic units. The lower one, termed the Margas Multicolores, is a thick series of sandstones, shales, and marls of continental origin. Predominantly shaly at the base, the sequence becomes sandy towards the top and is characterized by a persistent green band. The age of these beds is uncertain. Cockerell (1925), who described a species of the callichthyid catfish, *Corydoras*, from the Margas Verdes, a unit of the Margas Multicolores (Schlagintweit, 1937), assigned this specimen to the Tertiary or "even late Tertiary." The lithology and insect fauna associated with this second *Corydoras* occurrence appear to be identical with those of Cockerell. Harrington (1956) placed the entire Margas Multicolores in, and specifically assigned *Corydoras* to, the upper Cretaceous. Mammal fragments from the same horizon, although not the same locality, as *Corydoras* are Tertiary forms. Turtle bones from still another locality in the Margas Verdes are clearly no older than Oligocene (Williams, personal communication). Therefore, *Corydoras* evidently must be referred to the Tertiary. The presence of *Corydoras* in the Margas Multicolores supports Schlagintweit's (1936) opinion that most authors erred in assigning these beds to the Mesozoic.

Associated with *Corydoras* are numerous weevil elytra and internal molds of unidentified ostracods, which indicate, along with the lithology and the fish itself (Myers, 1938), a fresh-water origin for the deposit.

The upper stratigraphic unit which contains fossil fishes is separated from the Margas Multicolores by the Areniscas Superiores. The latter, formed primarily of varicolored sandstones and shales, is assigned to the

upper Miocene by Harrington (1956). The Areniscas Superiores is succeeded by the Terciario Subandino, a 4000-meter sequence of brownish red sandstones and reddish brown shales. These are capped by a few hundred meters of alternating conglomerates, sandstones, and shales considered to be upper Pliocene by Harrington. Three genera of fishes, a clupeid and two cichlids, occur in a finely laminated, light brown to chocolate-colored siltstone of the Terciario Subandino. Zunino assigns (personal communication to Schaeffer) the Terciario Subandino to the Miocene or Pliocene; Harrington placed these beds in the upper Tertiary,

TABLE 1  
STRATIGRAPHIC RELATIONSHIPS OF FOSSILIFEROUS BEDS  
OF SALTA PROVINCE, ARGENTINA

| Geologic Age    | Stratigraphic Unit                          | Fishes                                                     | Location        |
|-----------------|---------------------------------------------|------------------------------------------------------------|-----------------|
| Upper Tertiary  | Terciario Subandino                         | <i>Austroclupea</i><br><i>Aequidens</i><br><i>Acaronia</i> | La Yesera Creek |
| Middle Tertiary | Areniscas Superiores<br>Margas Multicolores | <i>Corydoras</i>                                           | Rio Cañas       |

above the Miocene. La Yesera Creek, from which these fossils come, is indicated as Miocene-Pliocene on the Geologic Map of Argentina (Dirección General de Industria Mineral, 1950). Information at present is insufficient to allow a more accurate dating of these beds.

Lithologic characteristics and the presence of cichlids suggest that La Yesera is a fresh-water deposit. The association of clupeid and cichlid is unusual, but not previously unknown. Although most clupeids are marine fishes, a few enter fresh water. Likewise, cichlids survive in salt water.

Table 1, developed from the sources noted above, shows the probable stratigraphic relationships of the fossiliferous beds.

## TAXONOMY AND DESCRIPTIONS

### ORDER ISOSPONDYLI

### SUBORDER CLUPEOIDEI

### FAMILY CLUPEIDAE

### AUSTROCLUPEA, NEW GENUS

GENOTYPE: *Austroclupea zuninoi*, new species.

GENERIC DIAGNOSIS: Ovate-oblong fishes differing from other clupeids

in the following combination of characters: Trunk short, head about one-third of standard length. Mouth moderate, about as in *Harengula*, somewhat superior, without teeth. Vertebrae, 35–37. Dorsal fin with 13–14 rays, situated closer to the snout than to the base of caudal fin. Pelvic fin seven-rayed, originating below middle of dorsal. Anal fin with 15–17 rays. Approximately 20 ventral scutes, all strongly keeled. Notochord not completely constricted. Scales without transverse grooves.

***Austroclupea zuninoi*,<sup>1</sup> new species**

TYPE: Y.P.F.<sup>2</sup> No. 19660, complete fish, crushed flat.

REFERRED SPECIMENS: About 200 fishes, many of them almost complete, but flattened.

HORIZON AND LOCALITY: Tertiary Subandino, La Yesera Creek, Salta Province, Argentina. This stream, flowing into the Juramento River about 60 miles northwest of Metán, is located in the vicinity of latitude  $25\frac{1}{2}^{\circ}$  and latitude  $26^{\circ}$  S. and approximately longitude  $65\frac{1}{2}^{\circ}$  W., on the Tucuman sheet of the Map of Hispanic America.

SPECIFIC DIAGNOSIS: Same as for genus.

DESCRIPTION: These are small clupeids. The body is oblong, compressed, and slightly deepened in the region of the abdomen. The following measurements and proportions are based on 20 fishes representing the more complete specimens. They indicate a standard length of about 21–39 mm. and a total length of about 28–52 mm. The body depth is included somewhat more than three times in the standard length.

The head comprises about one-third of the standard length in specimens of intermediate and large size. This proportion is somewhat lower in the smaller specimens. The head is approximately triangular in outline. The preorbital length is about one-quarter of the head length and somewhat less than the diameter of the orbit which is included about three and one-half times in the head. The parasphenoid is bowed ventrally at the level of the orbit, but the extent and shape of its posterior wings cannot be determined. The vomer is probably toothless. The moderate-sized gape is somewhat superior and inclined upward from a parallel to the long axis of the body. As is characteristic of all clupeids, the dentary is short and deep. The jaw articulation is behind the middle of the orbit. Teeth are not present on the dentary. Unfortunately, the shape and extent of the premaxillary and maxillary cannot be determined, nor can the presence of supramaxillary bones be ascertained. The characteristics of these bones

<sup>1</sup> Named in honor of Dr. Juan J. Zunino, Chief of Exploration, Yacimientos Petroliferos Fiscales.

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would be particularly helpful in a comparison of *Austroclupea* with living clupeids. The operculum is about twice as high as deep. It has a strong dorsoventral ridge on its anterior border, but otherwise its surface is smooth.

The total vertebral count is about 35–37, of which 20–22 are abdominal and 16–18 are caudal. A low, longitudinal ridge is present on the vertebrae. The pleural ribs are distinctly grooved and almost completely enclose the body cavity. Epimeral and hypomerall ribs are clearly present.

The significant characteristics of the dorsal and pelvic fins are stated in the diagnosis and require no further comment here. The anal fin is short and originates well behind the dorsal. The caudal fin is strongly forked and comprises 20 principal rays preceded by a number of short rays dorsally and ventrally.

Strong ventral scutes with long posterior processes extend from a point anterior to the pectoral fin to the anus. These total about 18–20, of which nearly half are post-pelvic in position. The scutes are inserted just anterior to each pleural rib by a vertical arm approximately 3 mm. long. The posteriorly directed, exposed part of the scute is about 2 mm. long. Anterior to the dorsal fin are seven ( $\pm 1$ ) supraneurals.

The body scales are cycloid and about twice as long as deep. There is no evidence of a lateral line. The posterior edge of the mid-body scales bears about a dozen short, longitudinal grooves. The lateral surface of the scale shows no transverse grooves.

**RELATIONSHIPS:** *Austroclupea* is assigned to the Clupeidae on the basis of the ventral keeled scutes, the prolonged bases of the two median caudal fin rays (Hollister, 1936), and the absence of a lateral line. The short anal fin, cycloid scales, and ventral scutes suggest that it must be included among the Clupeinae.

*Austroclupea zuninoi* is clearly distinct from the other known fossil clupeids of South America. *Clupea*, from marine Oligocene beds in Venezuela, is represented by isolated scales (Leriche, 1938) showing several transverse grooves. *Scombroclupeoides* described by Woodward (1908) from the Cretaceous of Brazil differs especially in the presence of anal ridge scales, fewer rays in the anal fin, and a jaw articulation that does not extend beyond the anterior limit of the orbit. In addition, there are two genera of double-armored clupeids, *Diplomystus* and *Knightia* (Schaeffer, 1947a).

Some comparisons may be made with those clupeids that most closely approach *Austroclupea*. These are members of the subfamily Clupeinae, clupeid fishes with short anal fins, ventral scutes, and low vertebral counts such as characterize the genera *Harengula*, *Rhinosardinia*, and *Sprattus*. No

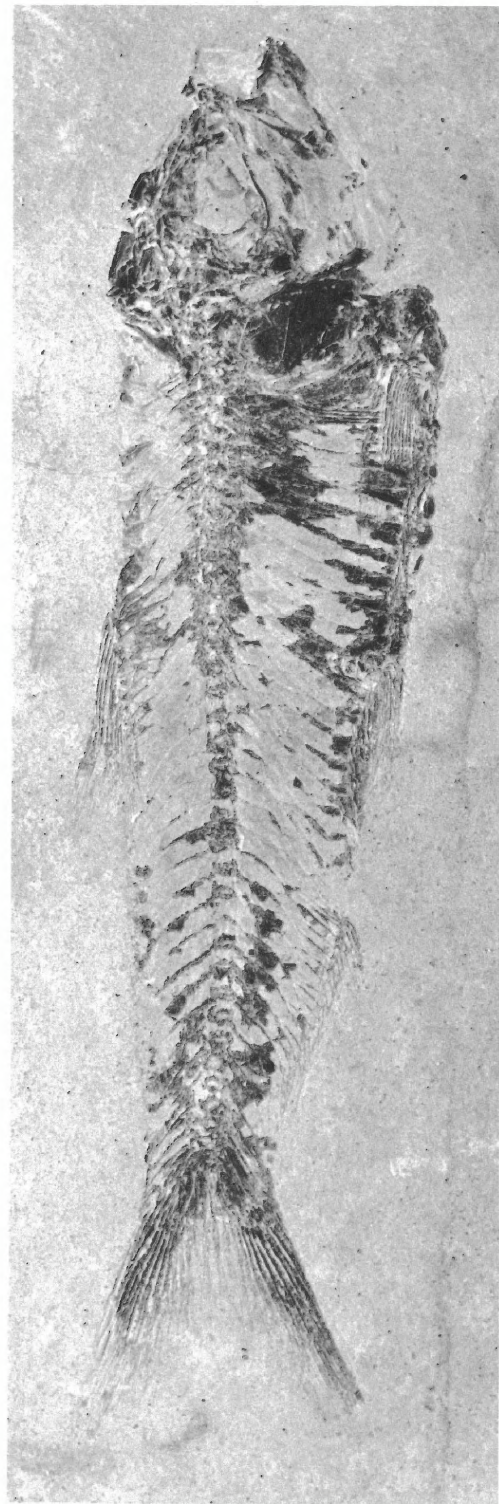


FIG. 1. *Austroclupea zuninoi*, new species, lateral view of type specimen, Y.P.F. No. 19660. Approximately  $\times 3.2$ .

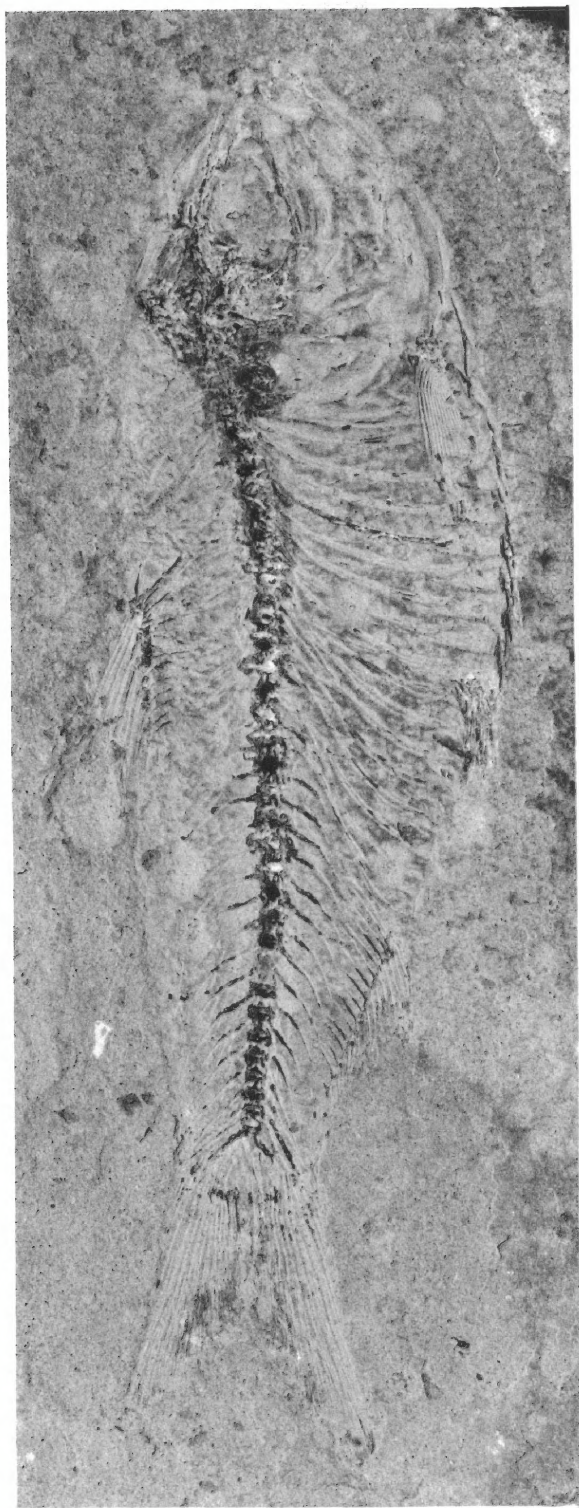


FIG. 2. *Austroclupea zuninoi*, new species, lateral view, Y.P.F. No. 19661. Approximately  $\times 3.2$ .

genus of this subfamily is restricted to the fresh waters of South America. However, several of the clupeines found along the South American coast may enter fresh water. Two genera of the subfamily Pristigasterinae are found in the rivers of South America, in some cases thousands of miles from the seas they also inhabit. But these differ from *Austroclupea* in having an elongated anal fin, a high vertebral count, and a projecting lower jaw (Norman, 1923).

In general shape and size, *Austroclupea* is similar to young specimens of living *Harengula*. It is possible, but doubtful, that the specimens of *Austroclupea* represent young fishes. Gunter (1957) noted that in cases in which marine fishes are taken in fresh water, they are predominantly the younger individuals of the species. As clupeids are primarily marine, *Austroclupea* may represent such an occurrence. However, the degree of ossification and the size of the orbit, even in the smaller specimens, probably indicate the adult condition. It is more likely that the small size of *Austroclupea*, in comparison with other clupeids, represents an adaptive response to the restrictions of a lake environment.

*Rhinosardinia*, from the southeast coast of South America, is a more elongated fish than *Austroclupea*, the head being included four and a half to five times in the body length (Regan, 1917b). The body form of the two species of *Sprattus* (separated from *Clupea* by Svetovidov, 1952) from the southeast coast of South America is more elongated than that of *Austroclupea*. As nearly as can be determined, the proportions of head to standard length and body to standard length in *Austroclupea* fall within the lower range of the variation noted in harengulids (Storey, 1938).

The skulls of *Austroclupea* are not well enough preserved to permit a detailed comparison of structure and proportions with Recent species of clupeids. The preorbital length of *Harengula* has about the same proportion to head length as in *Austroclupea*. The orbit is larger in proportion to the head. The mouth appears to be longer in *Austroclupea* than in *Rhinosardinia*, in which the articulation is in front of the middle of the orbit. The snout in *Rhinosardinia* is more elongated, and the lower jaw has a deeper chin.

The vertebral number in living clupeids is higher than in *Austroclupea*. While a considerable range of variation exists in the number of vertebrae of most genera in this family, the range, as far as known, of vertebral variation in the living South American clupeids does not include the number found in *Austroclupea*. An increase in the vertebral count of certain teleost lineages through geologic time is recognized (Schaeffer, 1947b). Early clupeids may have had a somewhat lower vertebral count than later forms, although the evidence is not so clear as in the Acanthopterygii.

Many isospondyl families which appear early show high vertebral counts, and these have been retained. Unfortunately, inadequate fossil clupeid material and uncertainty about their geologic position have made it difficult to trace changes in vertebral counts in this group. The low vertebral count in *Austroclupea* perhaps indicates the retention of a primitive feature. *Rhinosardinia* has 40 vertebrae. Regan (1917b) placed the number at 39, although it certainly must vary. In *Harengula*, the range is between 40 and 44. Regan (1917a) states that *Sprattus melanostoma* possesses 43 vertebrae.

The dorsal fins of all the clupeid genera considered have about an equal number of rays, the range of variation in one species of *Rhinosardinia* including the range of *Austroclupea*. The pelvic fin of *Harengula* has eight rays, a character that would exclude the fossils from this genus, for this number has been considered characteristic of *Harengula* (Storey, 1938). As in *Austroclupea*, the pelvic fin of *Harengula* is inserted behind the middle of the dorsal. In *Rhinosardinia* the pelvic fin is inserted in front of the dorsal, and it has eight rays. *Sprattus* agrees with *Austroclupea* in the number of rays in the pelvic fin. This is the only living clupeid from South America with seven pelvic rays. However, the dorsal fin in *Sprattus* is closer to the base of the caudal than to the snout, and the pelvics are inserted before it.

The number of prepelvic scutes in all known clupeids is considerably higher than in *Austroclupea*. But the number of these scutes might be expected to increase with a rise in the vertebral count (if such has occurred) and thus approximate that of the existing genera.

Mid-body scales of *Austroclupea* show no transverse grooves. The body scales of *Rhinosardinia* have a single transverse groove (Regan, 1917b), with an unsculptured posterior edge. In *Harengula* the mid-body scales show three to seven transverse grooves. The number of longitudinal grooves on the same scales varies widely among different species of *Harengula* and includes the number found in *Austroclupea*.

Although primarily a marine fish, *Harengula* enters brackish water, and one species is found in fresh water (Rivas, 1950). *Rhinosardinia* occurs in both marine and fresh water. Regan (1917a) stated that a specimen of *Sprattus melanostoma* was obtained from the Rio La Plata. Whether this represented a catch somewhat upstream in fresh water, in the bay, or a significant distance oceanward was not indicated.

From a consideration of the body size and the shape, the position of the fins in relation to the snout and the tail and to each other, as well as proportions of the head, it is not possible to identify these La Yesera fossils with any known clupeids living or fossil. Therefore these fossils are placed in a new genus.

Several features of *Austroclupea* are also significant taxonomic characters of a number of Recent clupeids which are considered generically distinct, which emphasizes the difficulty encountered in classifying fossil clupeids.

Recent clupeid genera have been defined on a suite of characters the evolutionary and functional relationships of which to one another have not been considered. Among the characteristics that have been used to separate modern genera are: the presence or absence of palatine and vomerine dentition; the number of supramaxillary bones; the position of the dorsal fin in relation to the pelvic fin and the number of rays in the pelvic fin; the characteristics of the last two anal fin rays; the position of the gill rakers; the ornamentation of the scales; the presence or absence of a notch in the center of the upper jaw; and the position of the mouth and length of the posterior wings of the parasphenoid (from Regan, 1917a; and Svetovidov, 1952).

Among fossil clupeids it is difficult to find the diversity of features mentioned above well enough preserved for adequate comparison with those of Recent clupeid genera. If modern clupeid genera were defined by a suite of characters the functional interrelationships of which had been demonstrated, it might then be possible, through a study of those features customarily preserved in fossil forms, to deduce the correlated structures and then assign fossil clupeids to an appropriate group.

ORDER OSTARIOPHYSI  
SUBORDER SILUROIDEA  
FAMILY CALLICHTHYIDAE  
GENUS *CORYDORAS* LACÉPÈDE

GENOTYPE: *Corydoras geoffroy* Lacépède, 1803.

*Corydoras revelatus* Cockerell, 1925

TYPE: B.M.N.H.<sup>1</sup> No. P.13679, almost complete fish, with part of head and anterior portion of post-cranial armature missing.

HORIZON AND LOCALITY: Margas Verdes at Cañas River, Salta Province, Argentina. This stream, a tributary of the Juramento River, is about 40 miles northeast of the town of Metán.

REFERRED SPECIMENS: Y.P.F. No. 19665, complete specimen; Y.P.F. Nos. 19666, 19667, two specimens of skull roof; also numerous fragments, mostly isolated lateral scutes, and some almost complete cuirasses.

REVISED SPECIFIC DIAGNOSIS: Range of standard length, determined

<sup>1</sup> British Museum (Natural History).



FIG. 3. *Corydoras revelatus*, dorsolateral view, Y.P.F. No. 19665. Approximately  $\times 4$ .

from the two complete specimens (figures for Cockerell's specimen noted first), 27–32 mm.; range of total length, 31–38 mm. Depth at base of dorsal fin, 9 mm.; orbital width, 2 mm.; snout length, 3.5 mm. Dorsal fin I,6; anal I,6. Caudal forked with 18 branched rays and about five dorsal and ventral raylets. No visible adipose fin. Lateral scutes consist of 23 dorsals and 22 ventrals.

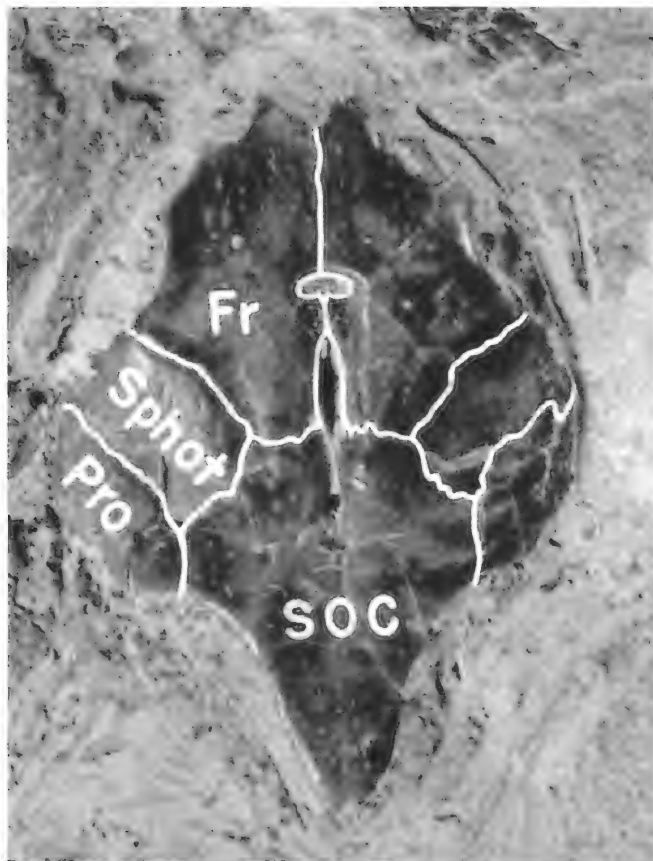


FIG. 4. *Corydoras revelatus*, dorsal view of skull roof, Y.P.F. No. 19666. Abbreviations: fr. frontal; pto, pterotic; soc, supraoccipital; sphot, sphenotic.  $\times 7.5$ .

**RELATIONSHIPS:** On the basis of Gosline's (1940) review of the family Callichthyidae, it is evident that this form should be assigned to the genus *Corydoras*. It can be distinguished from related genera by the dorso-ventrally compressed form of the body and head, the superior location of the eye, the elongated fontanel, and the composition of the dorsal fin. Although the dorsal fin on the fossil form has one less soft ray than the

lowest number indicated for the living species of *Corydoras*, the number is considerably fewer than that for *Brochis*, a closely related genus. A comparison of the dermocranium of the fossil and Recent species of *Corydoras* shows only slight differences in the suture patterns. The suture between the supraoccipital and the frontal, sphenotic, and pterotic bones is clearly shown in the three Cañas River specimens. In each, although the suture pattern varies slightly, the topographic arrangement of the bones is similar. An examination of skulls of two species of Recent *Corydoras* shows similar variation. The taxonomic value of these patterns, if any, must await more thorough study of a larger series. No pronounced differences are seen in bone shape or size between fossil and Recent forms.

The Cañas River specimens resemble those described by Cockerell (1925) from Sunchal in Jujuy Province, Argentina. The body of the Salta specimen is somewhat longer, but the body depth is about the same as or slightly greater than that of Cockerell's, when crushing is taken into account. The Cañas River specimens agree exactly in orbit and snout length with the Sunchal specimen. The dorsal spine, although strong, does not appear so robust as that in Cockerell's fish. The strong similarities between the fossils from these two areas far outweigh the slight differences and support the conclusion that these fossils are conspecific.

The discovery of *Corydoras revelatus* in Salta represents the second known occurrence of this species. A closely related fish, *Corydoras micracanthus*, is found in Salta Province at the present time (Regan, 1912). This represents the edge of the southwestern range of this genus in South America. Specimens of this species are not available for comparison with the fossil forms.

#### ORDER ACANTHOPTERYGII

##### SUBORDER PERCOIDEA

##### FAMILY CICHLIDAE

##### GENUS *AEQUIDENS* EIGENMANN AND BRAY, 1894

GENOTYPE: *Acara tetramerus* Haeckel, 1840.

##### ***Aequidens saltensis*, new species**

TYPE: Y.P.F. No. 19668, part and counterpart of nearly complete specimen, lacking ends of caudal and pectoral fins.

REFERRED SPECIMENS: Y.P.F. No. 19670, part and counterpart of head and anterior portion of body; Y.P.F. No. 19669, body, showing proximal portions of dorsal, caudal, and anal fins.

HORIZON AND LOCALITY: Tertiary Subandino, La Yesera Creek, Salta



FIG. 5. *Aequidens saltensis*, new species, lateral view of type specimen, Y.P.F. No. 19668. Approximately  $\times 1.5$ .

Province, Argentina. (See further description of locality under *Austroclupea*, above.)

**SPECIFIC DIAGNOSIS:** Ovate-oblong cichlid fishes of medium size. The standard length of the single complete specimen is about 10.7 cm.; its greatest depth, about 4.9 cm. Skull somewhat less than one-third of total body length. Vertebrae 27–28; abdominal 11–12, caudal, 16. Dorsal fin XIII,13; pectoral fin 13–14 (?); pelvic fin I,5; anal fin III,8. Caudal peduncle about as long as deep. Scales finely ctenoid.

**DESCRIPTION:** In shape, *Aequidens saltensis* resembles the short-bodied members of the genus such as *A. tetramerus*. The body is laterally compressed and rather deep, being included about two and one-half times in the standard length.

The mouth is small and terminal. The lower jaw articulates below the anterior border of the orbit. The mandible does not appear to protrude beyond the premaxillaries. The ascending processes of the moderately prehensile premaxillaries end just below the top of the orbit. Both the premaxillaries and the mandible are supplied with small conical teeth. The supraoccipital crest is strong, extending anteriorly to the forward margin of the orbit. Parietal crests form strong ridges above the eyes. The diameter of the eye is contained about four times in the length of the head. The eye thus appears to be relatively smaller than that of Recent species of *Aequidens*. Pharyngeal teeth are present on one specimen, but their pattern and number are indeterminable. The preoperculum is large and stout, its ventrolateral border ornamented with a few ridges radiating posteriorly and ventrally.

From the point of attachment to the skull, the vertebral column ascends sharply before turning downward in a gently descending curve. This form is characteristic of other members of this genus. The division between abdominal and caudal portions of the vertebral column differs from that of *Aequidens tetramerus*, for which Regan (1905) states that there are 13 abdominal and 13 caudal vertebrae. The centra are robust, and parapophyses appear to be developed on some abdominal vertebrae. The ribs and neural spines are strong.

The dorsal fin commences slightly behind the anterior border of the operculum and extends to the posterior end of the anal fin. In the living species of *Aequidens* and *Cichlasoma*, the dorsal fin begins somewhat more posteriorly, but still above the opercular cleft. The spines of this fin are of continually increasing length to the last which is about one-half of the length of the head. The base of the spiny dorsal is one and one-half times as long as the soft portion, while in the Recent species of this genus, it is two or more times as long. The soft rays are distorted distally, and their

length cannot be determined. Their number exceeds by one that indicated by Regan (1905) for the *Aequidens* group. The anal fin begins opposite the soft dorsal. The anal spines are very stout. The pectoral fin is poorly preserved, and the number of rays composing this fin is somewhat uncertain as is the length of the fin. The pectoral fin is inserted laterally about one-third of the distance between the ventral and dorsal borders of the body. The total form of the caudal is indeterminable, as the tip has been destroyed.

Ctenoid scales are scattered about the matrix near the fishes, but no pattern of their distribution on the body can be determined. The cheeks and opercular area are scaled.

RELATIONSHIPS: The deep body, the number of dorsal and anal fin spines and the number of vertebrae indicate that the Salta specimens may be assigned to the genus *Aequidens* as described by Regan (1905).<sup>1</sup> *Aequidens* differs from *Acaronia*, according to Regan, chiefly in the smaller posterior processes of the premaxillary, and from *Astronotus* in the smaller number of vertebrae and of soft rays in the dorsal and anal fins.

Schaeffer (1947a) described a single fossil cichlid as *Aequidens pauloensis* from the ?Pliocene of Brazil. Up to the present time this was the only reasonably complete fossil representative of this genus known. *Aequidens saltensis* is a somewhat smaller fish, with fewer dorsal spines and soft rays. The point of division of the dorsal fin in *A. pauloensis* into spiny and soft rays is unknown, but the total number of rays exceeds by three that of *A. saltensis*.

A comparison of the specimens from La Yesera Creek with the Recent and other extinct species of *Aequidens* indicates sufficient difference from them to warrant the erection of the new species, *Aequidens saltensis*.

GENUS *ACARONIA*<sup>2</sup> MYERS, 1940

GENOTYPE: *Acara nassa* Haeckel, 1840.

***Acaronia longirostrum*, new species**

TYPE: Y.P.F. No. 19664, part and counterpart of the head and anterior region of the abdominal area, crushed laterally.

REFERRED SPECIMENS: Incomplete specimens: Y.P.F. No. 19662, part and counterpart of the dorsal trunk region; Y.P.F. No. 19663, part and counterpart of the snout.

HORIZON AND LOCALITY: Tertiary Subandino, La Yesera Creek, Salta

<sup>1</sup> See Eigenmann (1910) regarding the taxonomy of *Acara*.

<sup>2</sup> Formerly *Acaropsis*. See Eigenmann and Allen (1942) for synonymy.

Province, Argentina. (See further description of the locality under *Austroclupea*, above.)

**SPECIFIC DIAGNOSIS:** Elongated cichlid fishes characterized by the following: an enlarged mouth extending laterally halfway along the elongated snout; gape, 1.5 cm.; premaxillaries, 2.5 cm. in length; vertebrae, 30? (13-14+16-17); dorsal fin, probably XIII, 13; pectoral fin, I,5; anal fin, III,7; scales ctenoid, those from the peduncle squarish, with six to eight basal radii.

**DESCRIPTION:** Although no complete individual is available, the specimens referred to this new species range from approximately 6 to 19 cm. in total length as determined from specimens with more or less complete vertebral columns. Most specimens seem to belong at the higher end of the observed size range. The body is elongated but not deepened. The caudal peduncle is strong and somewhat longer than deep.

The mouth is terminal, with a slightly projecting lower jaw. The 1.5-cm. gape, and the articulation of the lower jaw with the quadrate somewhat behind the anterior border of the orbit, indicate that this species has a somewhat larger mouth than other members of the *Aequidens* group. The premaxillaries are enlarged and very protractile. Their ascending processes extend well above the middle of the orbit. The maxilla is exposed to the level of the middle of the orbit. Small to fairly large conical teeth are present on the premaxilla and mandible in about three bands. The supraoccipital crest is moderately strong, not extending anteriorly beyond the middle of the orbit. The parietal crests are weak. The preoperculum is heavy. One specimen shows a few triangular ridges on its lateroventral border.

In correlation, perhaps, with the elongated body, the vertebral column does not show the same initial rise as does *Aequidens saltensis*, but the more posterior abdominal and the caudal vertebrae are similar in form and position. The centra are more robust and have a more pronounced lateral ridge. Also, the neural spines are stout and more posteriorly directed than those of *A. saltensis*.

The dorsal fin commences near the posterior border of the operculum and extends to about the end of the anal fin. Its spinous portion is strong. The soft rays on one specimen are at least 4 cm. long. The pectoral fin is poorly preserved but appears to be short. The caudal fin is broad and truncate posteriorly, with 18 principal rays.

The trunk is overlain with square ctenoid scales, most of which possess seven basal radii.

**RELATIONSHIPS:** The species *longirostrum* is tentatively placed in *Acaronia* primarily on the basis of the elongated, protractile premaxillaries, exposed

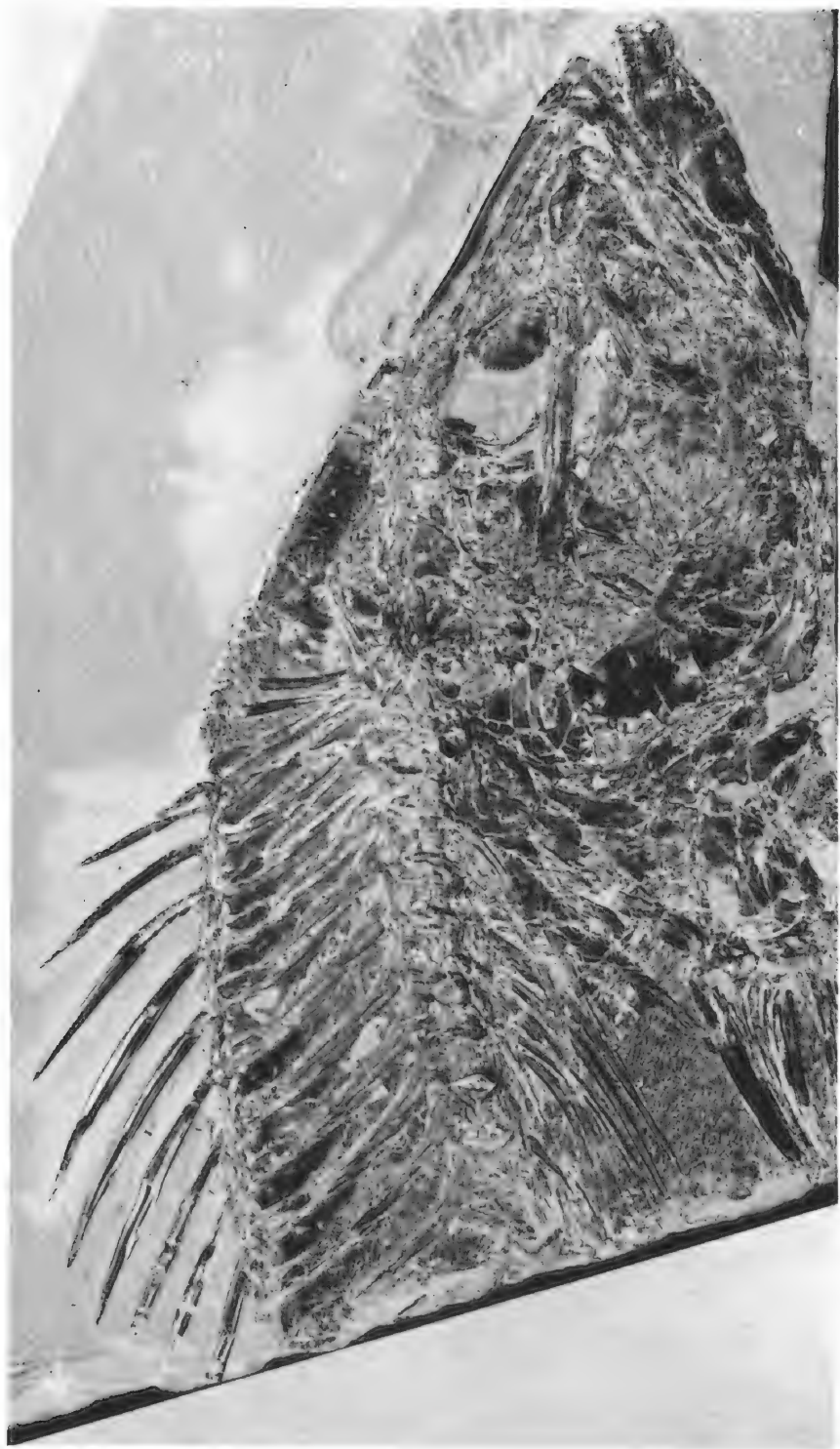


FIG. 6. *Acaronia longirostrum*, new species, lateral view of anterior portion of type specimen, Y.P.F. No. 19664. Approximately  $\times 1.75$ .

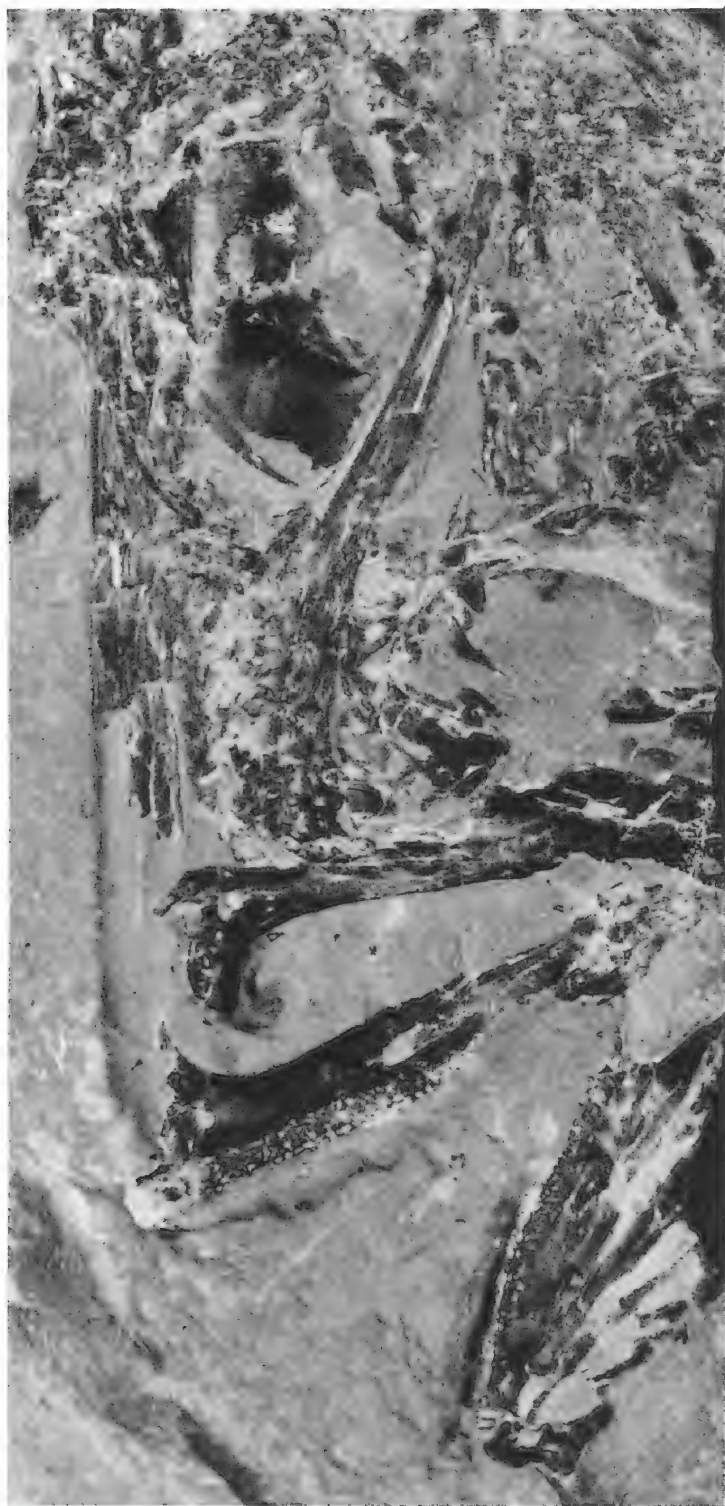


FIG. 7. *Acaronia longirostrum*, new species, lateral view of snout region, Y.P.F. No. 19663. Approximately  $\times 3.75$ .

maxillaries, reduced parietal crests, and large mouth. This genus is closely related to *Aequidens* and perhaps should be united with it. Until these genera have been investigated further, they are here regarded as distinct on the basis of the characters just cited (Regan, 1905).

*Acaronia longirostrum* differs from the Recent *A. nassa* in possessing a larger number of vertebrae and greater number of soft rays in the dorsal fin. According to Regan, there are 25 vertebrae and nine to 11 soft rays in *A. nassa*. The supraoccipital crest is larger than that in *A. nassa*. *Acaronia longirostrum* differs from *A. trimaculata* Eigenmann and Allen (1942) in possessing a strongly pointed snout, unequal jaws, a larger mouth, and a maxillary reaching the eye. A third species, from eastern Brazil, *A. rondoni* Ribeiro (1918), differs from *A. longirostrum* in having more dorsal and anal fin rays and a more varied dentition.

In regard to vertebral number, body shape, and snout elongation, *A. longirostrum* resembles *Geophagus*, but, unlike the latter, the maxilla is exposed, the mouth is large, and the jaws are unequal anteriorly.

In addition to the two cichlids described above, two other fossil cichlid genera are known from South America. One is a fragment, *Acara* sp. (Woodward, 1898), from the ?Pliocene of Brazil (Schaeffer, 1947a); the other is *Macracara prisca* described by Woodward (1939) from the lower Tertiary of Brazil. *Aequidens* can be distinguished from *Acara* by the presence of more rays in the soft portion of its dorsal fin (only the dorsal fin is known from Woodward's specimen) and from *Macracara* by the significantly fewer vertebrae, the lower number of dorsal fin rays, and the greater number of rays in the pectoral fin. Besides the features mentioned above, the long snout of *Acaronia* differentiates it from *Macracara*, in which the snout is short.

Another cichlid, *Cichlasoma* (Cockerell, 1923), is known from the Miocene of Haiti. It is separated from the *Aequidens* group by the presence of four spines in the anal fin.

No living cichlids are known from La Yesera Creek. This stream appears to be somewhat beyond the western range of modern cichlids which are mostly restricted to the lowlands to the east.

As modern cichlid genera have not been adequately diagnosed in terms of osteology, clearly distinct features of the fossil cichlids from La Yesera that indicate their association with particular Recent cichlid genera are difficult to ascertain. Judging by the similarity of La Yesera fossils to various living genera, the skeletal characters have changed little, and with our present knowledge are of limited value in separating closely related genera. Several genera of cichlids are at present found in one lake or river of South America. Such seems to be the case with the fossil assemblage

being considered.

In lieu of more restrictive cichlid diagnoses and more and better fossil material, it seems reasonable to assign this form with an elongated snout and enlarged premaxilla to the genus *Acaronia*, thus separating it from the closely related faunal associate, *Aequidens saltensis*.

## DISCUSSION

Tertiary fresh-water fish deposits are rare in South America. There are two localities in Brazil, four in Argentina, and one in Colombia. The fishes found at each locality are given in the list that follows. For purposes of the discussion the list is arranged in what may be the geological sequence of the various deposits, from the youngest to the oldest. The geologic position of the fossil fishes is somewhat dubious, as material is lacking for correlation with dates based on mammalian faunas. The list is based partly on the taxonomic similarity of each fossil assemblage to the modern South American fish fauna and in part on the geologic position assigned to the locality by the describer. In this discussion Recent and fossil South American fresh-water fishes are compared in regard to taxonomic similarity and distribution. The data on the distribution of modern fishes are from Eigenmann (1910, 1927).

The Recent fresh-water fish fauna of South America is composed primarily of characins, catfishes, and cichlids, with several other groups contributing minor elements to the fauna. Each of the dominant groups is represented in the fossil record. Among the minor groups, serranids and lepidosirenids are represented.

1. Tremembé and Tabauté, São Paulo, Brazil (from Schaeffer, 1947a; Travassos and Santos, 1955)

- Characinidae

- Eobrycon*

- Astyanax*

- Curimata*

- Ariidae

- Arius*

- Serranidae

- Percichthys*

- Cichlidae

- Acara*

- Aequidens*

2. La Yesera Creek, Salta Province, Argentina

- Clupeidae

- Austroclupea*

- Cichlidae

- Aequidens*

- Acaronia*  
3. Upper Magdalena Valley, Department of Huila, Colombia (from Savage, 1951)  
Unidentified lepidosirenid and siluroids  
4. Rio Cañas, Salta Province, Argentina, and Sunchal, Jujuy Province, Argentina (from Cockerell, 1925)  
*Callichthyidae*  
*Corydoras*  
5. Cerro Mirador, territory of Chubut, Argentina (from DeSaez, 1941)  
*Callichthyidae?*  
*Bachmannia chubutensis*  
*Ariidae*  
*?Arius argentinus*  
Unidentified siluroids  
6. Nova York, Maranhão, Brazil (from Schaeffer, 1947a; Santos, 1946; Santos and Travassos, 1956)  
*Clupeidae*  
*Knightia*  
*Characinidae*  
*Procharax*  
*Lignobrycon*  
*Cichlidae*  
*Macracara*  
7. Cañadón Hondo, territory of Chubut, Argentina (from Schaeffer, 1947b)  
*Serranidae*  
*Percichthys*

1. Probably the most recent material, geologically speaking, is from the Tabauté and Tremembé beds in São Paulo, Brazil. The fishes found here are quite similar to Recent forms. This assemblage contains several characins, an ariid, a serranid, and two cichlids. There does not appear to be any ecological reason for the absence of fresh-water catfishes such as callichthyids. Two modern characin genera (*Astyanax* and *Curimata*), both new to the fossil record, have recently (Travassos and Santos, 1955) been described from these deposits. These authors have emphasized the similarity of fossil and recent fishes by splitting the genus *Eobrycon*, from these beds, into two modern genera. The strong resemblance to Recent species shown by the fossil characins, as well as the similarity exhibited by other vertebrates and invertebrates in the fossil fauna to modern groups, has led Travassos and Santos to suggest a Pleistocene rather than Pliocene (as per Schaeffer) age for the deposit.

2. The fishes from La Yesera Creek, Salta Province, Argentina, are considered upper Tertiary. The assemblage includes a clupeid and two cichlids described in this paper. The cichlids are both modern genera. This similarity to existing forms might indicate to a neoichthyologist that

these fossils are of quite recent date. It is possible, however, that, once established in South America, some genera have developed with only slight changes over long periods of time. For example, a living serranid, *Percichthys*, is known from the Eocene.

The presence of a fresh-water clupeine, *Austroclupea*, is interesting, as this subfamily does not occur in the present inland fauna of South America. The other fossil clupeids of South America are from late Cretaceous and early Tertiary marine and estuarine deposits in Brazil. These clupeids belong to groups markedly different from *Austroclupea*.

La Yesera has not yet yielded characins and catfishes. Catfishes are probably found in this region today and are also recognized as fossils from earlier beds in Salta. Characins are found in waters to the east of La Yesera Creek and perhaps extend into streams in the area of the fossil deposit. Although characins do not appear in the fresh-water deposits of Argentina, they may have been present. Woodward (1900) has identified as characinoid some fragmentary material from a Pliocene marine deposit at the mouth of the Parana River in Entrerios Province, Argentina.

3. Fragments of unidentified siluroids and a lepidosirenid have been reported from the late Miocene of Colombia (Savage, 1951). Similar material of a more recent date has been found in western Brazil (unpublished).

4. Earlier Tertiary deposits with fresh-water fishes include the *Corydoras* from Salta described herein and the *Corydoras* from Jujuy (Cockerell, 1925). Both are represented by abundant, if largely incomplete, material. However, no evidence of other groups of fishes was found at either locality.

5. Several siluroids, including an ariid and what is probably a callichthyid, have been cursorily described but inadequately dated by DeSaez (1941) from the territory of Chubut in Argentina.

6. An assemblage of fresh-water fishes from Nova York, Maranhão, Brazil, comprises a double-armored clupeid (*Knightia*), a cichlid (*Macracara*), and two characins (*Lignobrycon*, Santos, 1946, and *Procharax*, Santos and Travassos, 1956). All these genera are known only as fossils. Woodward (1939), who described the clupeid and cichlid, believed the deposit was of early Tertiary age. Schaeffer (1947a) tentatively considered it Pliocene. If these beds are older than those previously described, they contain the earliest known representatives of two of the major groups of South American fishes.

7. A serranid, *Percichthys*, has been recorded (Schaeffer, 1947b) from the Eocene of Chubut, Argentina. This, at present, is the most accurately dated of fresh-water deposits on this continent, and *Percichthys* is therefore

the earliest genus also known among modern South American fresh-water fishes.

#### GEOGRAPHIC DISTRIBUTION OF FOSSIL AND RECENT FISHES

The genera of characins, ariid, and cichlids recognized from Tremembé and Tabauté are within the range of the living species of the same genera. The serranid is beyond the present range of this species which is restricted to Patagonia and Chile.

The cichlids from La Yesera are probably just beyond the western edge of distribution of present-day forms. The clupeid from La Yesera is geographically isolated. While clupeids of the subfamily Pristigasterinae are found in the Amazon and other rivers, these fishes are significantly different from *Austroclupea*. Those clupeids that most closely resemble *Austroclupea* are found in marine waters off southeastern South America. The ancestors of *Austroclupea* may have entered northern Argentina (?and elsewhere) during the middle Miocene when brackish continental sediments, reflecting a fluctuating coastline (Weeks, 1947), extended into northern Argentina.

A Recent species of *Corydoras* is found in Salta and Jujuy, the same region in which the fossil forms were found. The siluroids from Chubut are considerably south of the range of existing forms to which they are closely related.

*Percichthys hondoensis* from Chubut is within the range of modern species of *Percichthys*.

In summary, the known fossil fishes generally occur within the area occupied by modern forms of the same group. However, the fossil catfishes and cichlids from Argentina are on the western margin of the present-day distribution of these fishes. Typically, catfishes and cichlids are found today in lakes and streams with abundant vegetation and a varied animal life. The arid upland in Salta where the fossil forms were found was probably at one time similar to the wet lowlands to the east. Possibly the late Tertiary uplift (Harrington, 1956) of these western marginal areas has resulted in a constriction of the western distribution of these fishes. This does not explain why *Percichthys* has been eliminated from its former northern range.

The important fossiliferous localities which bear fishes akin to the Recent forms are inadequately characterized ecologically. Schaeffer (1947a) states that the São Paulo and Maranhão deposits are lacustrine-fluvial. The two deposits described in the present paper are simply considered fresh water. Despite the general taxonomic similarity between fishes from river environments and those from lake environments of South

America, differences do exist. It might be of some value in determining the origin and dispersal of the South American fresh-water fishes if we could accurately describe ecologically the various fossil fish deposits.

The evidence is still inadequate for the origin of the fresh-water fish fauna of this continent to be determined. Schaeffer (1947a) has reviewed the question and no significant additional information has been added since 1947. Fossils from beds of the earliest Tertiary and late Cretaceous are needed. However, more recent material exhibiting close relationships to modern forms is gradually becoming known. It may become possible to understand the evolution of certain groups without, as yet, uncovering the evidence of the origin of the modern fauna.

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